The Great Ordovician Biodiversification Event (GOBE): definition, concept, and duration

THOMAS SERVAIS AND DAVID A.T. HARPER

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The Ordovician biodiversification has been recognized since the 1960s; the term ‘The Great Ordovician Biodiversification Event’, abbreviated by many as the ‘GOBE, has been used for the past 20 years. The conceptual development and terminology applied to this crucial episode in marine life signify its considerable complexity. The GOBE includes successive biodiversity phases of the pelagic and benthic biotas, possibly decoupled. Put simply, the GOBE can be seen as a sequence of diversifications of the planktonic (late Cambrian - Early Ordovician), level-bottom benthic (Early-Middle Ordovician) and reef communities (Middle-Late Ordovician), although the boundaries of these ‘events’ are diachronous (as for the entire GOBE), and it is logical to assume that these communities co-evolved and interacted. The GOBE also includes several Biotic Immigration Events (BIMEs), such as the ‘Richmondian Invasion’ and the ‘Boda Event,’ recoding the large-scale dispersal of taxa from one biogeographic area to another. The GOBE is thus the sum of the diversity trends of all individual fossil groups showing rapid increases, diachronously, during different intervals and across different regions. It thus spans the entire Ordovician, capturing the increasing total diversity of marine organisms during the period. The GOBE is not simply one, but many sequential events.

☐ Ordovician, diversity, biodiversification, plankton, benthos, reefs

Thomas Servais ✉ [thomas.servais@univ-lille1.fr], Univ. Lille, CNRS, UMR 8198 - Evo-Eco-Paleo, F-59000 Lille, France; David A.T. Harper [david.harper@durham.ac.uk], Palaeoecosystems Group, Department of Earth Sciences, Durham University, Durham, DH1 3LE, UK and Department of Geology, Lund University, Lund, Sweden.

The term ‘The Great Ordovician Biodiversification Event’ and its acronym GOBE are widely used in the literature. Paradoxically, despite its common currency, the origin of this term and its definition are poorly understood by the majority of earth scientists.

The Ordovician (c. 485 to c. 443 Ma) is the geological period that exhibits the most rapid and significant increase in the diversity of marine organisms, at lower taxonomic levels, during the entire Phanerozoic. This Ordovician biodiversification together with the older ‘Cambrian Explosion’ comprises an Early Palaeozoic marine radiation that, together with the Early Mesozoic radiation, is one of the two most significant biodiversifications, in terms of sheer numbers of new taxa, in the Phanerozoic (e.g. Erwin *et al*. 1987; Crame & Owen 2002; Harper 2006; Stanley 2016). While some authors have considered the ‘Cambrian Explosion’ and the Ordovician biodiversification as separate radiations, others have suggested that they are both part of a single extended radiation event, displaying different facets of the construction of a resilient ecosystem. This question of whether to separate or conflate both ‘events’ is part of an ongoing debate (e.g. Droser & Finnegan 2003, Servais *et al*. 2009) in particular within the context of research on the exact timing of the onset of the Ordovician biodiversification (e.g. Servais *et al*. 2016).

Both the ‘Cambrian Explosion’ and the Ordovician biodiversification are by no means short ‘events,’ but took place over several tens of millions of years. Although the Ordovician radiation was one of the most important, major turnovers in the evolution of the marine biosphere, it was not as spectacular as the ‘Cambrian Explosion’ in that no new phyla, with the possible exception of the Bryozoa, are recorded from the Ordovician, no new Bauplans were apparently invented. The ‘Cambrian Explosion’ is also much more widely known because of the publication of numerous remarkable discoveries of spectacular fossils from the famous Fossil-Lagerstätten, such as the Burgess Shale of the Canadian Rocky Mountains, Sirius Passet in Greenland, or the Chengjiang Biota in South China (Fig.1). Such spectacular Lagerstätten are less common in the Ordovician (e.g. Lefebvre *et al*. 2016). Compared to the Cambrian ‘Explosion’, the Ordovician ‘biodiversification’ is therefore less well known, at least by the general public.

Was the Cambrian radiation an ‘explosion’ or a ‘diversification?’ Or did an ‘explosion’ take place during the Ordovician? These are simply questions related to the taxonomic rank that is analysed. At the higher taxonomic levels, e.g. the origination of animal phyla, the ‘explosion’ took place during the Cambrian, because the majority of animal phyla first appeared in the fossil record during the Cambrian. But it was only during the Ordovician that the diversity of lower taxonomic ranks clearly ‘exploded’: the diversity of orders, families, genera and species escalated during the Ordovician, not the Cambrian (e.g. Eble 1998). Thus, the ‘Cambrian Explosion’ was the first appearance in the fossil record of most, if not all, animal phyla, while an ‘Ordovician explosion’ took place at lower taxonomic levels. However, the term ‘Ordovician explosion’ has never been proposed or formally introduced and the term is not used by the Ordovician community of palaeontologists and geoscientists.

The radiation of organisms is not only based on biodiversity measures. The Ordovician radiation also introduced a high number of important changes in terms of ecological structuring (e.g. Sepkoski & Sheehan 1983; Bush *et al*. 2007; Servais *et al*. 2010; Harper *et al*. 2015) and of biomass production (e.g. Payne & Finnegan 2006; Servais *et al*. 2016; Pohl *et al*., this volume): it was during the Ordovician that modern marine ecosystems were established, with almost the entire water column (and the entire oceans) filled with organisms, while during the Cambrian, marine life was mostly restricted to habitats near the sea-floor and in near-shore environments (e.g. Miller 2004).

The term ‘The Great Ordovician Biodiversification Event’ that is widely used today, and abbreviated by many scientists to the ‘GOBE,’ was described by Webby (2004a). However, many authors do not strictly follow his concept, and there has been an increasing misunderstanding of the concept of the term, which ignited, in the last couple of decades, an ongoing debate on the definition, the concept and the duration of the ‘Great Ordovician Biodiversification Event.’ In addition it is now clear that the GOBE is not one but a family of sequential events rooted in the Cambrian, unfolding during the Ordovician.

The objective of the present paper is to review the history of the definition of the Great Ordovician Biodiversification Event (GOBE), to highlight its many interpretations and misinterpretations and to clarify its concept and duration.

Historical review and definition of the ‘Great Ordovician Biodiversification Event’ (GOBE)

The Ordovician biodiversification was clearly recognized in the 1960s and 1970s by a number of workers, who distinguished the Ordovician radiation from the Cambrian Explosion (e.g. Valentine 1969, 1973). Subsequently, Sepkoski (1978, 1979, 1981, 1984, 1988, 1991, 1995, 1996, 1997) established without doubt the statistical reality of the Ordovician biodiversification with respect to a range of different phyla with diverse life modes. The

‘Ordovician radiation’ was thus named and defined for the first time during the 1980s (e.g. Sepkoski & Sheehan 1983). It was clearly understood as an adaptive radiation of the marine fauna and this was clearly addressed in the landmark contribution by Sepkoski (1995) at the Seventh International Symposium on the Ordovician System (ISOS) at Las Vegas, Nevada, USA. In a subsequent paper, Droser *et al*. (1996) used the term in their seminal paper ‘The Ordovician Radiation’. The term, ‘Ordovician Radiation,’ was largely used during the 1990s and early 2000s (e.g. Miller & Mao 1995; Droser & Sheehan 1997; Miller 1997a, 1997b, Miller 1997c; Droser & Finnegan 2003; Miller 2004). However, it is noteworthy that Sepkoski (1995) had already recognised Ordovician radiations (in plural), rather than specifying a single Ordovician event.

Following the Las Vegas ISOS in 1995, three Ordovician palaeontologists, Barry Webby (Sydney, Australia), Mary Droser (Riverside, California, USA) and Florentin Paris (Rennes, France), proposed an International Geological Correlation Programme (IGCP) project entitled ‘*The Great Ordovician Biodiversification Event: Implications for Global Correlation and Resources*.’ This project was accepted and supported by UNESCO and the IUGS (International Union of Geological Sciences) and ran from 1997 to 2001, with an additional year (or extended term) in 2002, under the banner IGCP 410. The term ‘*Great Ordovician Biodiversification Event*’ was thus created and used by many scientists, participating in project 410. The Ordovician radiation became an ‘event’ in the context of many international geological projects in the last decades of the 20th century that were focused on ‘global events’ or ‘event stratigraphy’ (e.g. Walliser 1995). However, the only clear and unambiguous description of the term ‘Great Ordovician Biodiversification Event’ is that of Webby (2004a), in the introduction of the benchmark ‘Webby book’ that summarized the key contributions to IGCP project 410 (Webby *et al*. 2004a).

Webby (2004a, p. 2) introduced the volume by noting that the term ‘Great Ordovician Diversification Event,’ had been used during the years 1997 to 2002 but was also named the ‘Ordovician Radiation’ (Droser *et al*. 1996). He described the “Great Ordovician Biodiversification Event” as follows: ‘*Although the most intensive part of the Ordovician Radiation was during the Mid to Late Ordovician epochs, an interval of 28 m.y. (until the second extinction pulse of the end Ordovician mass extinctions) ... , some taxonomic groups (e.g., trilobites, inarticulated brachiopods, graptolites, conodonts, and rostroconch mollusks) also diversified significantly during the Early Ordovician. Consequently, all these evolutionary events from the beginning to virtually the end of the Ordovician Period—*

through nearly 46 m.y. of earth history should be treated as belonging to the Ordovician Radiation'.

Webby (2004a, fig. 1.1. A) illustrated the 'Great Ordovician Biodiversification Event' within the frame of the entire Phanerozoic, by utilising Sepkoski's key figure (1984, fig.1). In addition, he modified Sepkoski's figure 1 (1995, fig. 1) to illustrate an almost continuous increase of diversity during the entire Ordovician, from a base level at c. 489 Ma to immediately before the Late Ordovician Extinction Event (LOME; Finnegan *et al.* 2016), near the Ordovician– Silurian boundary at c. 443 Ma (Webby 2004a, fig. 1.1. B). Thus, the duration of the 'Great Ordovician Biodiversification Event' was also clearly described by Webby (2004a), effectively encompassing the entire Ordovician Period, of some 46 myr.

Webby (2004a) summarized in his introductory chapter the important data compiled by Ordovician specialists to construct the diversity curves of almost all fossil groups presented in the Webby *et al*. (2004a) volume. However, the absence of a synthetic figure, with a comparison of the diversity curves from the Webby *et al*. (2004a) volume, possibly explains why Webby (2004a) has not received greater attention. Similarly, the concept of the 'Great Ordovician Biodiversification Event', as described by Webby (2004a), as the sum of the individual biodiversification events of all fossil groups during the entire Ordovician, has not been strictly followed by many authors. The 'Boda Event' (*sensu* Fortey & Cocks 2005) or the 'Richmondian Invasion' (*sensu* Holland 2007) for example, are clearly part of the 'Great Ordovician Biodiversification Event', according to Webby's (2004a) concept. These events should not be considered as events that are separate from the 'Great Ordovician Biodiversification Event' (see below), but merely as constituent parts.

As described by Webby (2004a), the 'Great Ordovician Biodiversification Event' is the sum of many individual events. In the same volume, Miller (2004, p. 381) clearly pointed out the similarity with the concept of the 'Ordovician radiation': '*The impression emerging thus far from investigations of hierarchical patterns during the Ordovician (e.g. Patzkowsky 1995; Miller & Mao 1998; Adrain* et al. *2000) is that different scales of diversification were, in fact, characterized by unique signatures that may be indicative of unique processes not necessarily linked to one another'*. The 'Great Ordovician Biodiversification Event' is thus not a single event, but the sum of numerous, possibly disparate, events, either at different regional scales, at different temporal scales, or both. The 'Great Ordovician Biodiversification Event' could also be named the 'Great Ordovician Biodiversification Events,' in plural, similar to Sepkoski's (1995) use of the term 'Ordovician Radiations'. Similarly, it could be questioned if the 'Great Ordovician Biodiversification Event' can be named an 'event,' because the entire duration of it covered a time interval between 45 and 50 myr. It was certainly not a short 'event.' However, on the scale of the Phanerozoic, or the age of the Earth, it is, nevertheless, a unique, relatively short time interval.

The abbreviation (acronym) for the term 'Great Ordovician Biodiversification Event' was introduced later (following the publication of the Webby *et al*. 2004a volume) as 'GOBE' by several authors. About ten years after Webby's description (2004a), most authors were already using the acronym GOBE. This abbreviation is widely accepted today. It has been introduced in geology and palaeontology textbooks and is available to the general public.

Some 20 years after the intensive research on global events and event stratigraphy, is the definition still robust? Today, it is clear that the 'GOBE' was as much an 'event' as the 'Cambrian explosion' was an 'explosion'. However, both terms are very widely used. We therefore advocate the continued use of the term 'Great Ordovician Biodiversification Event' in the sense of Webby (2004a). We also propose to keep the usage of the acronym 'GOBE' for what is essentially the Ordovician radiation.

The Great Ordovician Biodiversification Event (GOBE) and Biotic Immigration Events (BIMEs)

Many different diversity curves have been drawn for the Ordovician. Such curves are either focused on individual fossil groups, different ecological groups or on different palaeogeographical areas ('palaeocontinents'). A few publications display global curves including all marine invertebrates (e.g. Sepkoski 1995, fig. 1; Webby 2004a, fig. 1.1.B). One of the most recent compilations, based on the Paleobiology Database (PBDB), illustrates the Ordovician genus-level diversity trend of occurrence data, compiled by Kröger & Lintulaakso (2017). This diversity curve (Fig. 2), confirming previous diversity trends, shows a continuous and sustained increase of diversity between the Early Ordovician (Tremadocian) towards the Late Ordovician (Sandbian and/or Katian). The increase of global diversity thus took place over a long period of time, between c. 485 Ma and c. 455 Ma, i.e., totalling an interval of about 30 myr. As the focus shifts, however, to an individual fossil group, or to specific palaeogeographic regions, shorter or more local events become more apparent. In addition, different pulses of different groups of organisms (planktonic, benthic, reef-building organisms) can be identified (Fig. 2), as explained below.

Event or events? GOBE versus BIMEs

Various authors have identified specific ‘events’ during the Ordovician and the Silurian. Significantly the term event has also been utilised for isotopic excursions (e.g. SPICE, DICE, and MDICE), and related to extinctions (such as the Late Ordovician Mass Extinction Event [LOME] in the Hirnantian), but the term ‘event’ is also used for biodiversification events, among them, for example, the ‘Richmondian Invasion’ or that associated with the ‘Boda Event’.

The ‘Richmondian Invasion’ is currently interpreted as a Biotic Immigration Event (BIME) (Stigall *et al*. 2017). BIMEs record the large-scale dispersal of taxa from one biogeographic area to another. The Richmondian Invasion (e.g. Holland 1997, Stigall 2010) was a regional scale BIME that prompted a substantial ecosystem turnover during the late Katian (Late Ordovician), when oceanographic changes facilitated inter-basinal migration into the Cincinnati Basin (Ohio, Kentucky, and Indiana) (Stigall *et al*. 2017). Another well known ‘event’ in the Ordovician is the ‘Boda Event’. Fortey & Cocks (2005) noted this short-lived warming event before the Hirnantian glaciation. The ‘Boda Event,’ named after the Boda Limestone in Sweden, resulted in the invasion of the high latitude, cooler waters by organisms that are usually known only from warmer (tropical water) environments. The ‘Boda Event’ is thus also a ‘Biotic Immigration Event ‘*sensu* Stigall *et al*. (2017).

Bearing in mind the concept of the GOBE by Webby (2004a) as the sum of the radiations that occurred during the Ordovician, it is logical to consider that the GOBE included several of these Biotic Immigration Events. Additional BIMEs will undoubtedly be identified in the future, completing the picture of the GOBE. However, single (regional) BIMEs are unlikely to be global events (in contrast to the GOBE), even if biodiversifications co-occurred on different continental margins.

Biodiversification(s) at the level of individual groups

Biodiversity curves assembled by the Ordovician workers in Webby et al. (2004a) were presented for some groups at the species-level, or as combined species- and genus-level diversity surveys (e.g. pelagic groups: graptolites, chitinozoans, radiolarians, and some benthic groups: bryozoans, sponges, stromatoporoids, echinoderms); while for other (larger benthic) groups they were mostly presented at the genus level (e.g. trilobites, brachiopods, gastropods, bivalves and nautiloids). For a variety of reasons most of the curves were rather incomplete at a global level, and it became immediately obvious that the diversifications of the individual groups took place at different times. This was highlighted by Webby (2004a, table 1.1.) in the introduction to the volume where he tabulated the number of taxa (genera and species) of all fossil groups that were used to compile the different diversity curves; he also compared them with the data analysed by Sepkoski (2002). In addition, Webby (2004a) summarized the patterns provided for every single fossil group, but he (and indeed subsequent authors) did not compile the different curves into a single diagram.

Following Sepkoski (1995), Webby (2004a) considered that the pelagic and benthic realms were possibly decoupled. Webby (2004a) noted that the timing of the major Ordovician radiations of the level-bottom and the reef communities were markedly different (Sheehan 1985, Webby 2002); the first diversified after the Early-Middle Ordovician boundary interval, the second only after the Middle-Late Ordovician boundary. Sepkoski was not able to include in his datasets all the planktonic groups, because data for some groups (including the phytoplankton) were not yet available. However, it is now evident, that in addition to the level-bottom and reef communities, there was a major diversification within the plankton much earlier than the Middle and Late Ordovician, with the possible onset of a plankton radiation as early as the late Cambrian, bolstered by a massive diversification of plankton communities after the Cambrian-Early Ordovician boundary (Servais *et al*. 2008, 2016).

Simplified (Fig. 2), the GOBE could thus be separated into three different phases comprising diversifications of the planktonic (late Cambrian - Early Ordovician), level-bottom benthic (Early-Middle Ordovician) and reef communities (Middle-Late Ordovician), although the boundaries (beginning and end) of these phases are diachronous (as for the entire GOBE), and it is logical to assume that these sets of communities co-evolved and interacted.

The GOBE, as a sum of diversifications of individual fossil groups, thus spans the entire Ordovician, with the increasing total diversity of marine organisms. The GOBE is the sum of the diversity trends of all individual fossil groups that show rapid increases at different intervals and across different localities. Not surprisingly, specialists of individual fossil groups have identified the 'GOBE' at different intervals.

The Plankton Revolution

The 'Plankton Revolution', marking the arrival in the fossil record of planktonic organisms (Servais *et al*. 2008), but also introducing planktotrophy near the Cambrian-Ordovician boundary (e.g. Nützel & Frýda 2003; Peterson 2005; Nützel *et al*. 2006) can be considered as the first major step of the GOBE with profoundly changed marine ecosystems, and a ‘revolution’ in the marine food chains (Figs 2, 3). Although several major planktonic groups only appear in the fossil record after the Cambrian-Ordovician boundary, the onset of the ‘Plankton Revolution’ took probably place in the late Cambrian (Servais *et al*. 2016).

The diversity of the phytoplankton, considered a key part of the base of the marine trophic chain, ‘exploded’ in the late Cambrian (e.g. Nowak *et al*. 2015), followed by a slow but continuous increase of phytoplankton diversity during the Early and Middle Ordovician (Servais *et al*. 2004, 2008). At a larger scale, phytoplankton diversity increased continuously from the early Cambrian to the Middle – Late Ordovician (Fig. 3), mirroring to some extent the biodiversity of marine invertebrates, at least during the Cambrian (Nowak *et al*. 2015), and possibly also during the Ordovician (e.g. Hints *et al*. 2010).

Planktonic graptolites appeared in the fossil record just after the Cambrian-Ordovician boundary (Fig. 3), and the first major peak of diversity is visible in the Floian (e.g. Crampton *et al*. 2015). The chitinozoans, considered to be derived from planktonic organisms, also first appeared during the Tremadocian (Fig. 3), and show their first important increase (based on data from Laurentia) in the early Floian, before further increases in diversity during the late Floian (linked to data from Gondwana) and the Dapingian (linked to data from Baltica). The global biodiversity curve of the chitinozoans clearly illustrates also the diversity pulses observed on the different palaeocontinents (Achab & Paris 2007).

Data on radiolarians, another major zooplanktonic group, remain incomplete, but a major turnover and a diversity increase took place during the late Cambrian (see Servais *et al*. 2016, and references therein).

A major phase of diversification in level-bottom communities

As indicated above, Sepkoski (e.g. 1995) and Webby (2004a) considered that diversity changes in the pelagic and benthic realms were possibly decoupled. A dramatic change in the level-bottom communities is observed during the Middle Ordovician, clearly after the onset of the ‘Plankton Revolution’ (Fig. 2). Among the benthic organisms, the brachiopods are the dominant group. They show a steep increase of biodiversity in the Darriwilian at the global level (e.g. Harper 2006, 2010, Harper *et al*. 2013, 2015), as illustrated in Fig. 4 . But the global curve has three main components: an Early Ordovician (Tremadocian-Dapingian) sector dominated by early orthoids and syntrophoids, a Middle Ordovician (Darriwilian) sector, overwhelmingly dominated by the rise of the plectambonitoids and strophomenoids and a Late Ordovician (Sandbian-Hirnantian) sector marked by the arrival of diverse groups of cyrtomatodont brachiopods (Harper *et al*. 2017). The early history and evolution of the phylum has, not surprisingly, a strong influence on the composition and shape of the curve. There are strong peaks reported from along the northern Gondwanan margin, during the Tremadocian, dominated by linguliform brachiopods ; at the same time the diversification of the Cambrian evolutionary fauna continued in shallow-water siliciclastic facies (Colmenar and Rasmussen, this volume). During the same interval in tropical Gondwana (South China), orthide and syntrophide faunas flourished prior to the massive spike in diversity during the Darriwilian (Zhan & Harper 2006).

Another group of (mainly) benthic organisms are the echinoderms. Following their appearance in the fossil record during the Cambrian, a much more significant echinoderm radiation commenced in the Early Ordovician, but diversity curves vary greatly across the five echinoderm subphyla (e.g. Sprinkle & Guensburg 2004). Blastozoan echinoderms, for example, show a more continuous slow increase between the late Cambrian and the Late Ordovician (Nardin & Lefebvre 2010). Crinozoans (crinoids), however, only diversified, substantially, during the Katian (Late Ordovician). For many other benthic groups, the datasets are not complete or not up to date (see also Servais *et al*. 2010), but it appears that the 'major pulse' of diversification of level-bottom communities was observed during the Middle Ordovician, and this major pulse was considered by some authors as the GOBE (see below).

Reef communities

Reef-building organisms diversified even somewhat later compared to planktonic and benthic organisms (Fig. 2), confirming previous observations (e.g. Sheehan 1985, Webby 2002). Figure 5 illustrates the diversity changes at a global level of different reef-builders. The most diverse group are the bryozoans. Ernst (this volume) demonstrates that the diversification of the bryozoans mostly occurred during the late Middle and early Late Ordovician, with a high peak in the Katian (over 130 genera recorded). Sponges diversified more continuously over the entire Ordovician, but only become highly diverse in the Late Ordovician (Carrera & Rigby 2004). Stromatoporoids were virtually absent during the Early Ordovician, and only increased significantly in diversity during the Late Ordovician (Webby 2004b, fig. 13.2). Corals show a rapid diversity increase after the Middle-Upper Ordovician boundary (Webby *et al*. 2004b, fig. 15.1), clearly emphasising that the 'GOBE' within reef-communities only occurred in the Late Ordovician.

To sum up, there is a progressive evolution of the different fossil groups, associated with unique short-lived events that cannot always be precisely located. The sum of these local diversity patterns and trends of all the fossil groups is essential to develop a complete picture of the GOBE.

Biodiversification(s) at the level of palaeobiogeographical provinces and 'palaeocontinents'

Miller (2004) highlighted the investigation of contrasts of the chitinozoan diversifications across several palaeocontinents (Paris *et al*. 2004), using consistent taxonomy and techniques, as an exemplar for the study of other fossil groups. Diversification phases occurred at different intervals across different palaeocontinents: the Gondwanan data from North Africa ('north Gondwana') illustrate a diversity peak in the Darriwilian (Paris *et al*. 2004, fig. 28.2), the diversity increase in Baltica is visible between the Dapingian and Darriwilian (Paris et al. 2004, fig. 28.3), and the diversification in Laurentia increased massively during the Katian (Paris *et al*. 2004, fig. 28.4), i.e. during the 'Richmondian Invasion.' Achab & Paris (2007) updated these data and depicted a global diversity curve for the chitinozoans that nicely illustrates that the global curve with its peaks is shaped by the regional trends.

Within the Brachiopoda the locus of diversity also switched during the Ordovician. Early radiations occurred on the South China Plate during the Tremadocian and Floian (Zhan & Harper 2016), with substantial diversifications at mid latitudes (particularly on Avalonia, Baltica and the island environments of the Celtic province) during the early Middle Ordovician. The appearance of significant numbers of rhynchonellides and spire-bearing brachiopods is associated with carbonate environments at low latitudes, especially on and around Laurentia.

Diversity curves including all marine invertebrates from different palaeocontinents also show different patterns. Hammer (2003) compiled biodiversity curves for Baltoscandia (palaeocontintent Baltica) that show a substantial increase in biodiversity, with a major increase commencing in the middle Floian, and more limited diversification events in the Middle and Late Ordovician. On the other hand, the analyses of the regional diversity trends from South China reveal a different pattern (e.g. Rong *et al*. 2007). The 'GOBE in South China' took place much earlier (e.g. Zhan & Harper 2006), with its onset in the late

Cambrian, and a dramatic increase of diversities mostly in the earliest part of the Ordovician (Rong *et al*. 2007, fig. 2-5). Was the 'Baltica GOBE' preceded by a 'Chinese GOBE' and then followed by a 'Laurentia GOBE?' Clearly these were regional constituents of the GOBE.

Miller & Mao (1998) compared the diversity trends in South China and Laurentia, and noted that global biodiversity curves must be dissected in order to understand biodiversity trends at all scales. Biotic factors may be of primary significance at one scale (e.g. the local, community level), whereas abiotic factors, such as orogenesis may have been of importance at another, larger scale (e.g. palaeocontinental scale) (Miller & Mao 1995, 1998).

Duration of the Great Ordovician Biodiversification Event (GOBE)

Classically, the 'Ordovician Radiation' (*sensu* Sepkoski) succeeded the Cambrian Explosion. The 'Great Ordovician Diversification Event,' as described by Webby (2004a), clearly spans the entire Ordovician, but usage of the term is not consistent. Previously published and most recent compilations of datasets indicate that diversity increased during the Early and Middle Ordovician, culminating in the peak diversity during the (early and middle parts) of the Late Ordovician (e.g. Kröger & Lintulaakso 2017). Following the middle Late Ordovician, global diversity declined. This decline was not as abrupt as previously assumed (with a rapid and dramatic extinction at the end of the Ordovician), but occurred over several myr, possibly due to long-term cooling associated with emerging icehouse conditions that started long before the Hirnantian (e.g. Nardin *et al*. 2011) (Fig. 6). The duration of the diversification at a global level thus spanned an interval of at least 30 myr: the GOBE is a long event!

The frequently cited and recycled figure of Trotter *et al*. (2008, fig. 3) illustrates a different view, with a much shorter duration of the GOBE. The compilations of 'Ordovician biodiversity pulses' are designed in order to show that the 'major biodiversity pulses' occurred during a relatively short interval in the Darriwilian, reflecting the 'level-bottom benthic' radiation (Fig. 2). Similarly, Schmitz *et al*. (2007) linked an asteroid breakup to the 'GOBE,' also considering that a relatively short interval in the Middle Ordovician represented the major phase of biodiversification at around 470 Ma (but see also Lindskog *et al*. 2017). However, this major pulse (also confirmed by Kröger & Lintulaakso 2017) is not the GOBE *sensu stricto* as described by Webby (2004a), based on Sepkoski's concept (e.g. 1995).

The onset of the GOBE and its components

Recognition and imposition of the original concept and definition of the GOBE poses a series of complex and interrelated, research questions. When precisely was the onset of the GOBE and how did it relate to the Plankton Revolution? As the event progressed when and where did the diversifications on Baltica, the Mid Ordovician hotspot (Rasmussen *et al*. 2007), and the diversifications associated with the Boda Event (or other BIMEs) originate? Locating the origins and the triggers (biotic and abiotic, i.e. intrinsic and extrinsic factors) of the GOBE and its expression at local, regional and global levels and across the taxonomic groups depends on the concept of the GOBE (and its constituent parts).

During 1997-2002, the members of the International Geological Correlation Programme (IGCP) 410 '*The Great Ordovician Biodiversification Event: Implications for Global Correlation and Resources*' mostly focused on the datasets and the diversity trends of individual fossil groups. It was the following project 503 '*Ordovician Palaeogeography and Palaeoclimate'* (2004-2009) that attempted to find the triggers of the GOBE (Harper *et al*. 2011), while project 653 '*The onset of the Great Ordovician Biodiversification Event*' (2016-2020) sought the beginning of the radiation.

The 'Plankton Revolution' was probably triggered by global oceanographic changes (Algeo *et al*. 2016, Servais *et al*. 2016) and/or increasing sea-levels (Fig. 6), and possibly by an oxygenation event (Saltzman *et al*. 2011), but it is so far not understood why planktonic organisms suddenly diversified during the late Cambrian – Early Ordovician.

The massive increase in the diversity of level-bottom benthic organisms, clearly visible in the datasets, appearing somewhat later (with major pulses in the Darriwilian), similarly requires explanation. Tectonic or oceanic triggers or biological factors have been proposed. Stable isotope excursions (Fig. 6) have been introduced in the debate as well (e.g. Munnecke *et al*. 2010; Algeo *et al*. 2016) as proxies for environmental change. Was it the presence of (phytoplankton) food that became available that fuelled the diversification of the benthos (e.g. Bambach 1993; Martin 2003; Martin et al. 2008) or did primary production and the biomass in the ocean increase and, if so, to what extent (e.g. Payne & Finnegan 2006, Pohl *et al*. this volume)? Were the changing palaeo-oceanographic conditions (e.g. Servais *et al*. 2014, Pohl *et al*. 2016) or a general global cooling responsible for the radiation (e.g. Trotter *et al*. 2008; Nardin *et al*. 2011; Rasmussen *et al*. 2016), possibly triggered by the appearance of land plants and the resulting decrease of $p\mathrm{CO}_2$ (e.g. Lenton *et al*. 2012)?

Significantly, land-plant organisms are usually not integrated in current datasets and diversity trends that are typically limited to marine invertebrates (but see also Masuda &

Ezaki 2009). Nevertheless, major changes within the terrestrial ecosystems took place during the Ordovician (e.g. Rubinstein *et al*. 2010, Gerrienne *et al*. 2016): land-plant derived cryptospores from bryophyte-like plants become widespread in the Middle Ordovician, forming a 'bryophytic landscape' (Fig. 6). In the Late Ordovician, the first trilete spores probably indicate the arrival of tracheophytes (vascular plants). An important algal-plant transition occurred during the Cambrian – Early Ordovician interval. When was the onset of the biodiversification of the land-plants, in the Middle Ordovician or much earlier and what factors triggered the evolution of land-plants? This opens up the question as to how the terrestrial and marine realms are linked.

A final question revolves around the substantial occurrence of reef-building groups developed in the Upper Ordovician. Did Ordovician palaeogeography and palaeoclimate change substantially in order to trigger the dominance of metazoans? Or, more controversially, was it the presence of a superplume, as postulated by some (e.g. Barnes 2004; Lefebvre *et al*. 2010) that prompted these changes? As for all the other Phanerozoic radiations the answers are complex.

Conclusion

The Great Ordovician Biodiversification Event (GOBE) is part of a substantial and sustained radiation of marine animals, that commenced during the Cambrian Explosion and climaxed during the Devonian Nekton Revolution (Klug *et al*. 2010). The GOBE, by definition, includes diversifications during the entire Ordovician and is a combination of a range of more local regional radiations within individual taxonomic groups, across a range of environments, partitioned by the distinctive geography of the period. BIMEs had a key role at more regional levels. The complex patterns and trends at local, regional and global levels indicate a variety of drivers and facilitators (both extrinsic and intrinsic) that combined to initiate and sustain this remarkable event.

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Figures and captions:

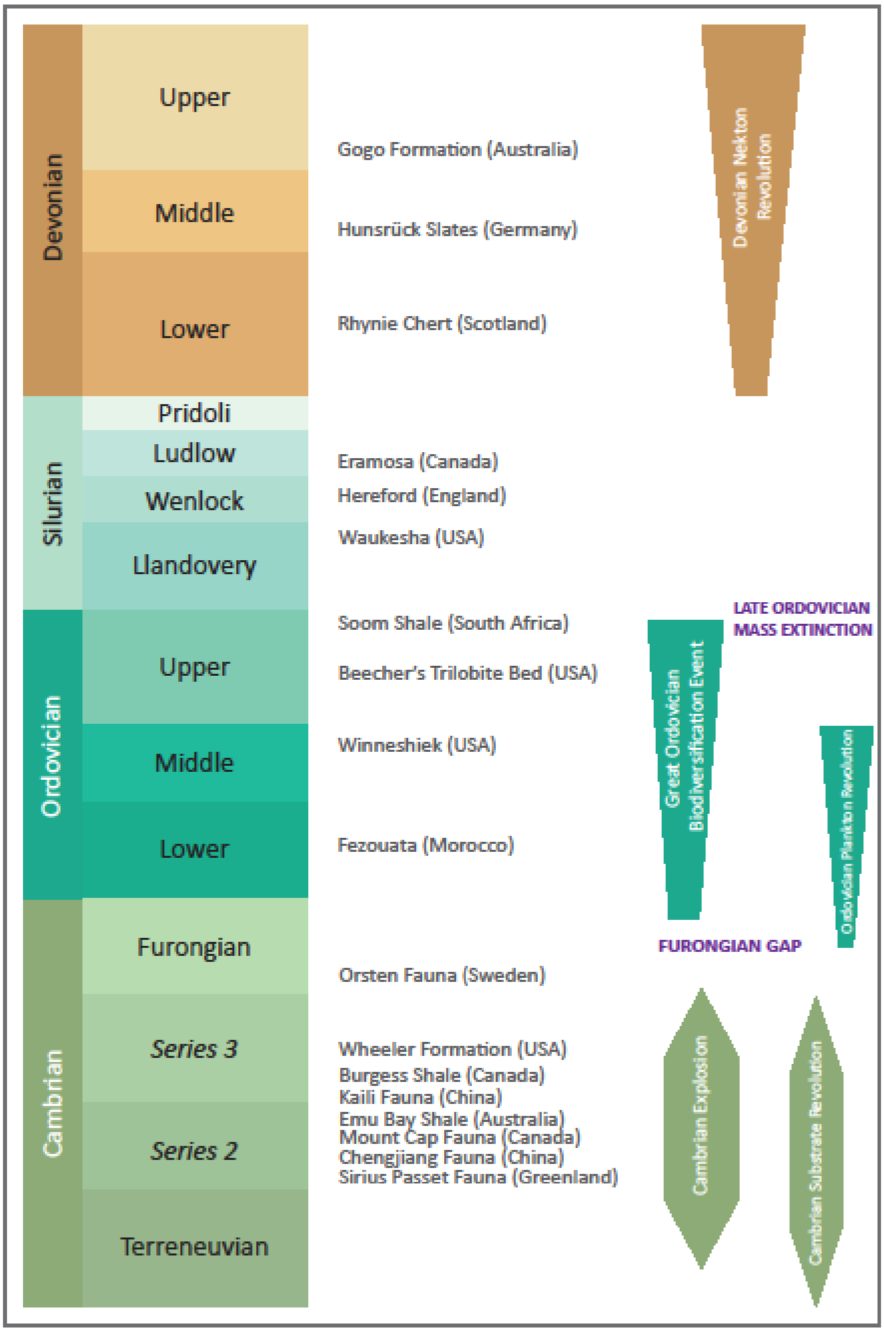

Figure 1: Stratigraphic distribution of the main Fossil-Konservat-Lagerstätten in the Lower and Middle Palaeozoic (Cambrian – Devonian). For the definition of the terms Cambrian Substrate Revolution, Ordovician Plankton Revolution and Devonian Nekton Revolution, the reader is referred to Bottjer *et al*. (2000), Servais *et al*. (2008, 2010), and Klug *et al*. (2010) respectively. The 'Furongian gap' is the late Cambrian interval with low diversities of fossil marine invertebrates between the Cambrian Explosion and the Great Ordovician Biodiversification Event.

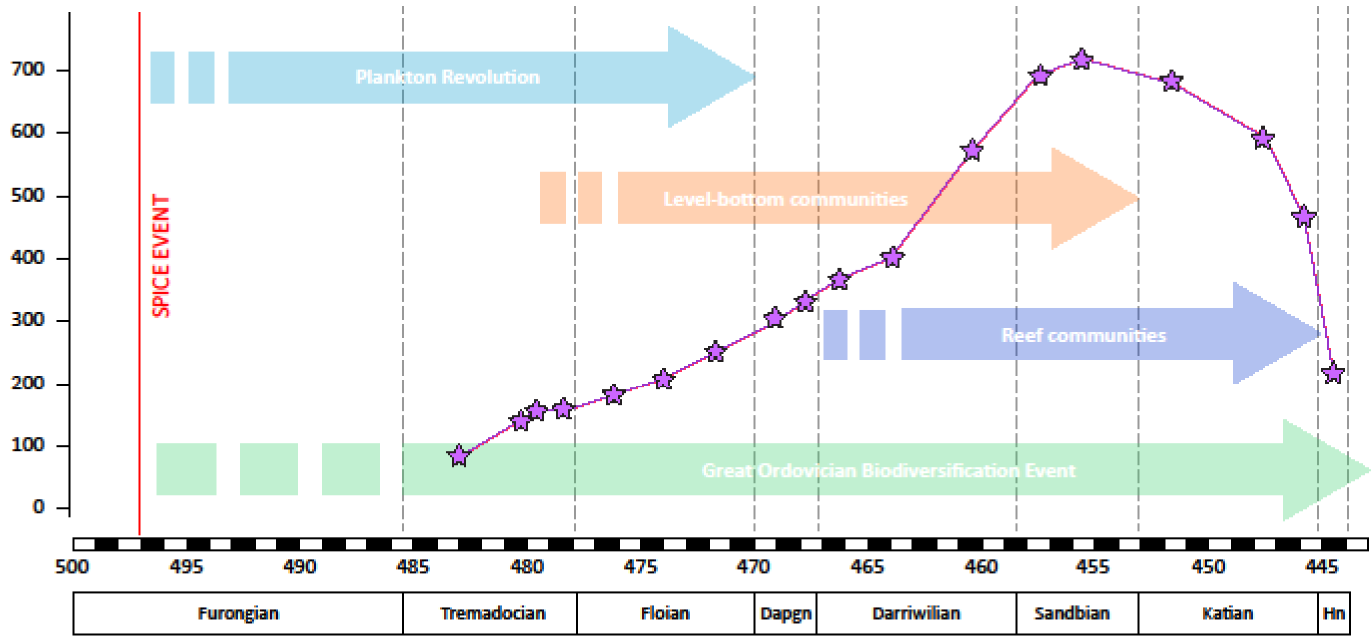

Figure 2: The Great Ordovician Biodiversification Event illustrated by the genus-level diversity trend of occurrence data, compiled by Kröger & Lintulaakso (2017). Three distinct phases of diversifications represent the planktonic, benthic and reef-building organisms. For explanations see text.

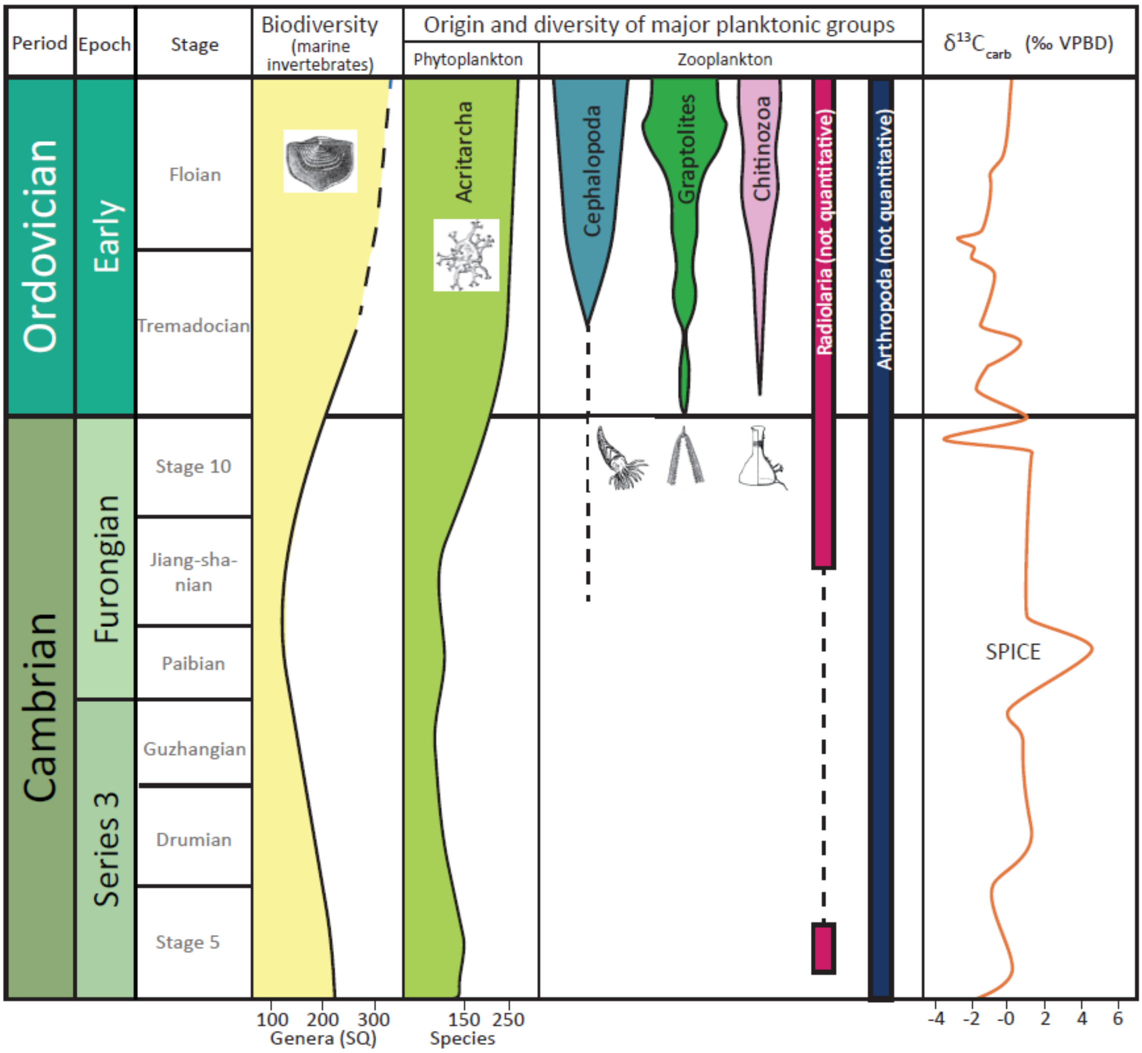

Figure 3: The onset of the 'Plankton Revolution' in the late Cambrian, illustrated by middle-late Cambrian–Early Ordovician biodiversity estimates, modified after Servais *et al*. (2016).

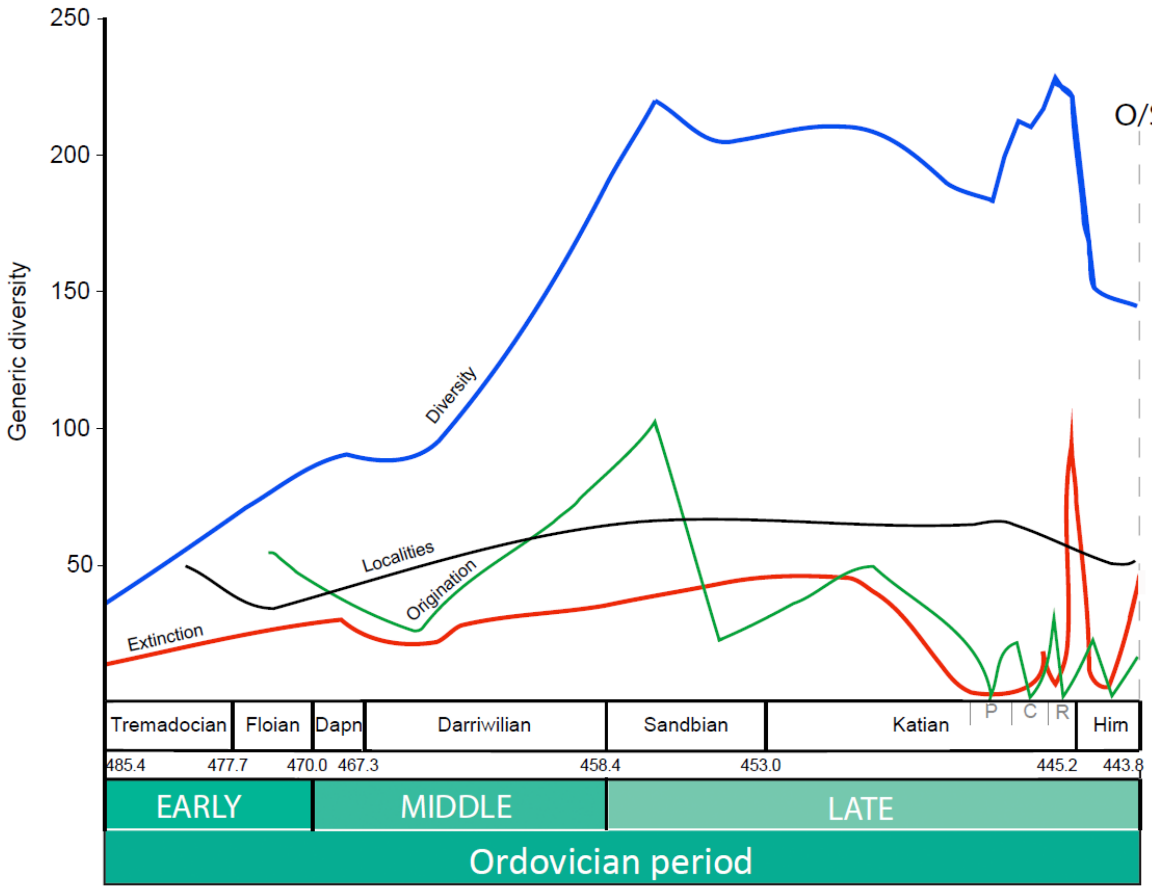

Figure 4: Ordovician generic brachiopod diversity, illustrating changing diversity through the seven Ordovician time slices, indicated by maximum number of genera and maximum number of localities together with extinction and origination curves, modified after Harper *et al*. (2013, fig. 11.1.).

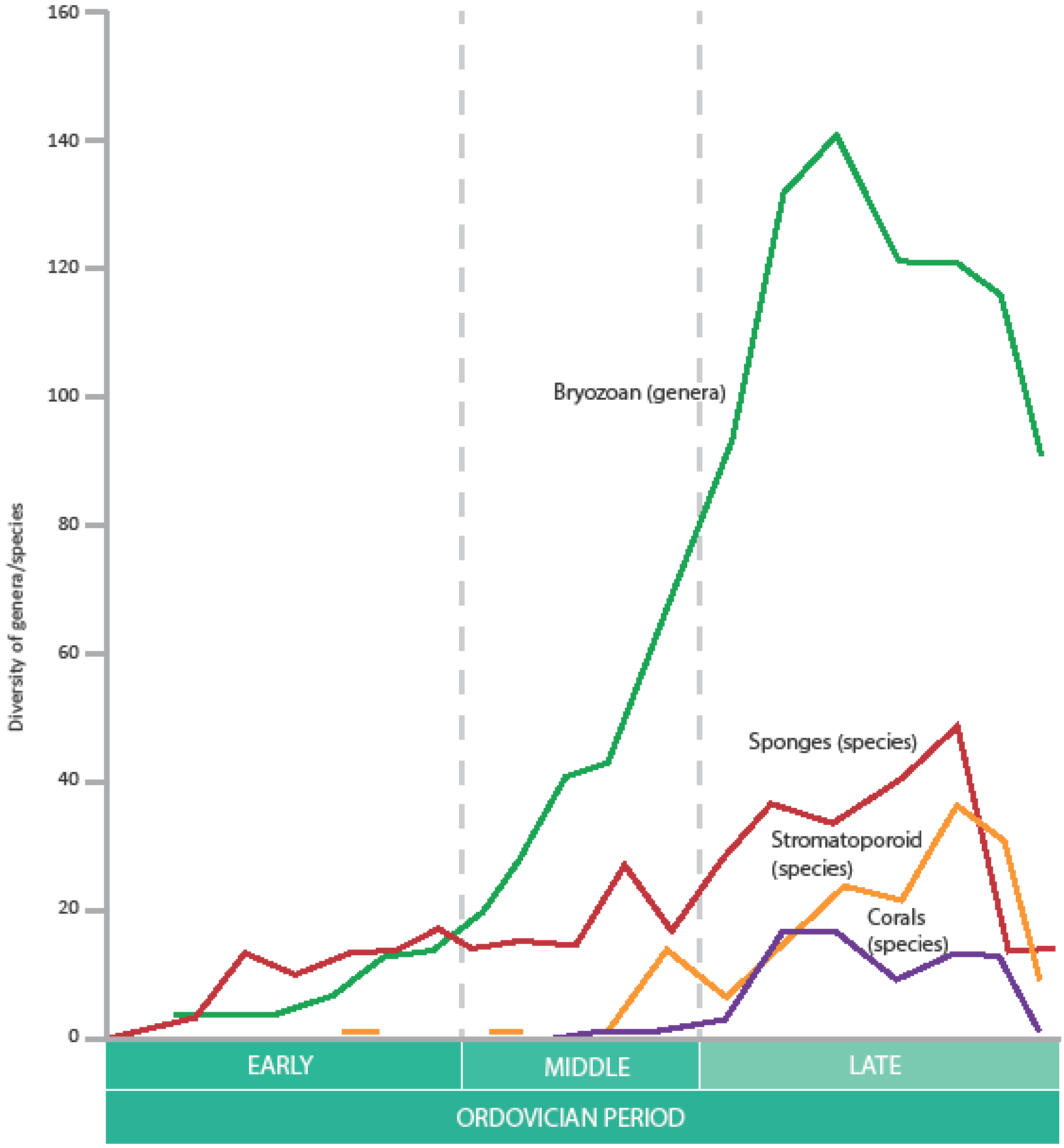

Figure 5: Diversity trends during the Ordovician of reef-building organisms. Generic bryozoan diversity based on Ernst (this volume), specific sponge diversity based on Carrera &

Rigby (2004), specific stromatoporoid diversity based on Webby (2004b), specific coral diversity based on Webby *et al*. (2004b).

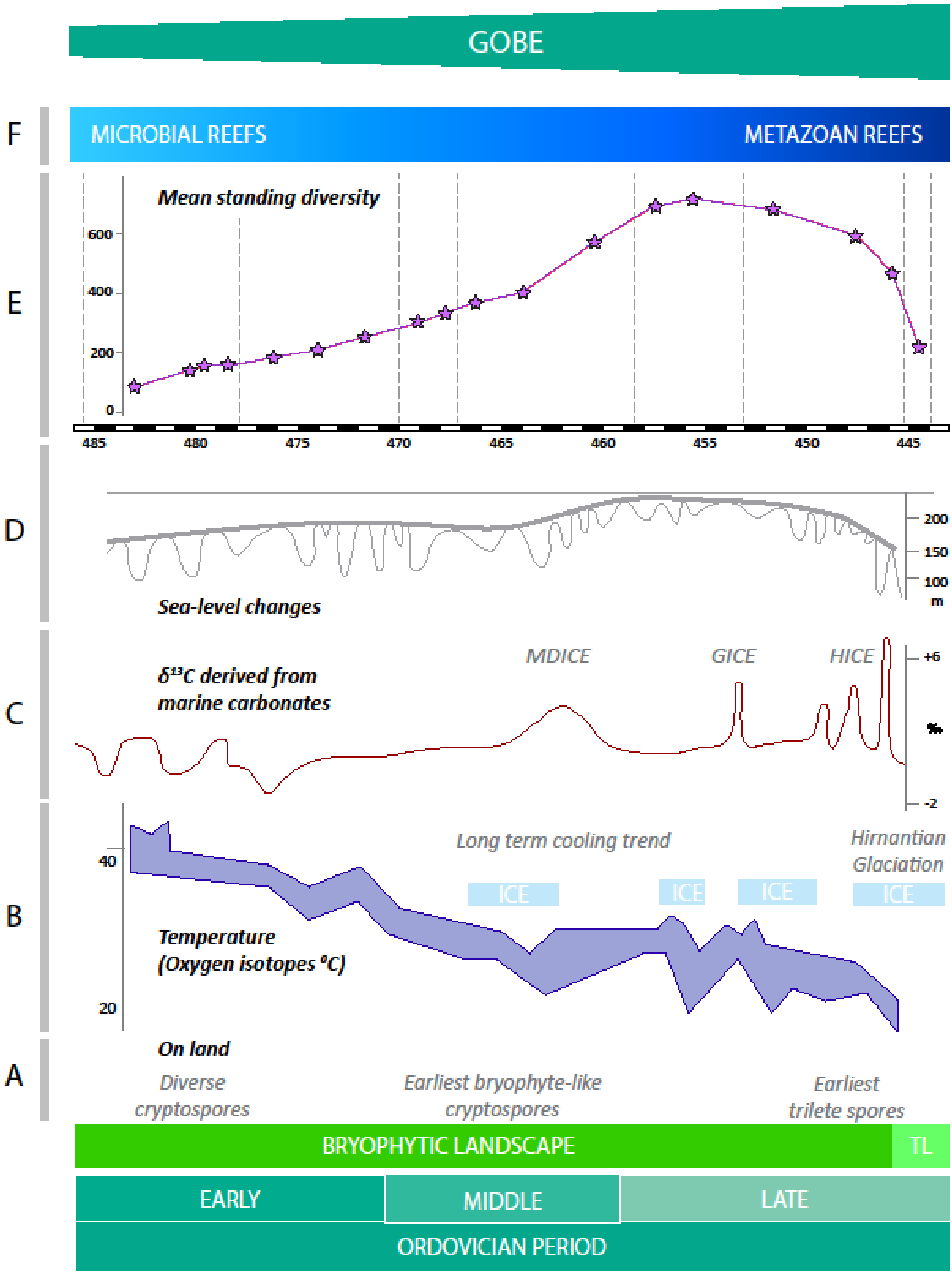

Figure 6: Synthesis of the Great Ordovician Biodiversification Event, modified after Algeo *et*

al. (2016). Mean standing diversity of marine invertebrates compiled by Kröger & Lintulaakso (2017); sea-level curve after Haq & Schutter (2008); carbon isotope curve after Bergström *et al*. (2009); long term cooling trend after Nardin *et al*. (2011), evolution of land-plants after Gerrienne *et al*. (2016). HICE: Hirnantian carbon isotope excursion; GICE : Guttenberg carbon isotope excursion; MDICE: mid-Darriwilian carbon isotope excursion.